# THE GROWTH AND SHELL MICROSTRUCTURE OF THE THECIDEACEAN BRACHIOPOD *MOORELLINA GRANULOSA* (MOORE) FROM THE MIDDLE JURASSIC OF ENGLAND

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ABSTRACT. Analysis of the growth habit of *M. granulosa* from a functional point of view has proved to be of value in the interpretation of shell microstructure. Serial sectioning of shells at 20 μ intervals has revealed that fibre orientation may change suddenly at various levels within a shell. The paper notes the need for detailed information regarding the orientation and location of sections through shells, as study of *M. granulosa* indicates this may be of critical importance. The shell-structure differs markedly from that of *Lacazella mediterranea* (Risso), as the shells of some, if not all Inferior Oolite thecidellinids were differentiated into primary and secondary layers. Interpretation of the microstructure has taken into account the effects of shell resorption in the brachial valve and the development of crescentic tubercles in the pedicle valve. Some evidence has been obtained which indicates that the pedicle opening of *M. granulosa* occupied a supra-apical position. Despite the general spiriferoid appearance of the shell-structure, the detailed microstructure of various morphological features of the two valves, together with bulk morphological similarities, are thought to suggest strophomenoid affinity.

THE microstructure outlined in this paper is based on combined evidence from serial sections and polished blocks prepared from fifty-three specimens, comprised of brachial valves, pedicle valves, and complete shells of *Moorellina granulosa* (Moore), from the Oolite Marl of Westington Hill Quarry in the Cotswolds. The stratigraphy and location of the quarry and the exact horizon from which the material was obtained have been described in a previous paper (Baker 1969). A further horizon has been located in a yellow-orange clay at the base of the Oolite Marl on the west face of the quarry but the material recovered was not sufficiently well-preserved for the study of shell microstructure.

In the material studied, many of the shells are recrystallized but some are well preserved. Partially recrystallized material is useful for comparing and contrasting the unaltered shell with diagenetic effects.

A discussion of the thecideacean environment and a detailed account of the morphology of the brachial valve (Pl. 18, fig. 1) is given in an earlier paper (Baker 1969).

The most prominent feature of thecideidines is the elaboration of the brachial apparatus. The inevitable result of interest in this structure is that in much of the published work the pedicle valve is neglected.

The pedicle valve of thecideaceans is subject to much less variation than the brachial valve and the pedicle valve of *M. granulosa* (Pl. 18, fig. 2) is morphologically very similar to that of *Bifolium faringdonense* (Dav.), described by Elliott (1948). Attachment to the substratum is by cementation and the shape of the pedicle valve is greatly influenced by the size of the scar of the area of attachment. Ontogenetic development of the valve concerns the appearance and development of crescentic tubercles, the change in position of the hinge teeth and the change in the relative proportion of the hemispondylium.

The shell of *M. granulosa* is endopunctate and shows the apparently random distribution noted by Elliott (1955). However, neither the models proposed by Kemežys (1965) nor Cowen (1966), satisfactorily explain the punctation mosaic observed in thecidellinids. An account of the punctation mosaic and the proposal of a new model is to be published separately.

During analysis of the microstructure, particular care has been taken to attach significance only to structures seen in at least six different specimens. Occasional peculiar features are noted which may be important but occur so infrequently in the material studied that firm conclusions must not be drawn from them.

## PREPARATION OF MATERIAL

A comprehensive account of the preparation of Oolite Marl material is given in Baker (1969) and the material studied in the present paper was obtained by the same method. For microstructure investigation however, it has been discovered that reduction of the etching time from ten seconds in 5 % HCl, to eight seconds in 3 % HCl yields better results. In addition it was found that fresh resin does not make a good bond with plain glass slides and blocks may become detached during sectioning. A more effective bond is obtained by the use of ground glass slides.

## GROWTH AND DEVELOPMENT OF THE SHELL

*General*. The nature of shell growth is mixoperipheral, leading to a strophic condition (Rudwick 1959, p. 18), as, contrary to the belief of Elliott (1965), a small hypercline dorsal interarea (by definition, Williams 1965, H59) is present (Pl. 18, fig. 5). The lateral profile is obscured by the area of attachment but in forms with a small area of attachment, may be described as modified plano- to concavo-convex with a rectimarginate commisure. Certain differences in the development of structures in the brachial and pedicle valves have taxonomic significance and they will be discussed separately, following an account of the general shell growth.

A comprehensive account of shell deposition in living brachiopods is given by Williams (1956, 1966, 1968*a*, *b*), Williams *et al*. (1965) and it is reasonable to suppose the shell of *Moorellina granulosa* (Moore) was deposited in the same manner. Evidence presented in this paper shows that Williams (1968*a*) is in error in regarding the single layered shell of *Lacazella mediterranea* (Risso) as typical of the thecideidine shell structure. *M. granulosa* clearly shows the development of primary and secondary shell layers.

As described in an earlier paper (Baker 1969) the brachial valve of *M. granulosa* is initially almost circular, later becoming broader than long. However, study of a number

of specimens shows that the shape of the brachial valve is really controlled by the shape of the pedicle valve, which is itself strongly influenced by the size of the scar of the area of attachment. Williams (1956) has shown that although cell division occurs throughout the epithelium the enlargement of the brachiopod shell is controlled mainly by peripheral zones of growth.

Various aspects of the mode of shell growth have been defined by Rudwick (1959, p. 2). It is convenient for the purpose of demonstrating the mode of growth in *M. granulosa* to use his second interpretation, i.e. that the shell surface represents a series of sectors which were formed continuously by different arcs of the valve edge.

At a magnification of $250\times$ linear, the external surface of the shell of well-preserved specimens of *M. granulosa* is seen to be covered with small fibres. These fibres are inclined radially outwards from the umbo at a low angle from the shell surface and show an orientation normal to the growth-lines and commissure (Pl. 18, fig. 3). If one assumes that the fibres are associated with the deposition of primary shell, either mechanically or crystallographically, their orientation directions may be used as growth vectors for the determination of points of relatively rapid increase in various arcs of the commissure.

Rudwick has shown how growth at any point on the valve edge may be resolved into component growth rates. By assigning a value of one growth unit to an arbitrary surface area corresponding to Rudwick's growth points (1959, text-fig. 1*a*), provided that the growth vectors are known, different rates of growth in different sectors of a shell can be fairly accurately determined. To demonstrate this adequately in *M. granulosa* necessitates the introduction of additional 'momentary' and 'cumulative' terms. The growth vector may be regarded as the cumulative product of the arrangement of growth units normal to the mantle edge. The total number of growth units per growth vector may be represented as $d/\sqrt{x}$, where $d$ represents the length of the vector and $x$ represents the surface area of the growth unit. *Proliferation points* occur where the distance between two growth vectors has doubled and *proliferation arcs* are represented by lines joining series of new proliferation points. The growth rate in any sectors may be determined by the *growth acceleration*, $v$, which is represented by the number of proliferation arcs in any sector. The *relative growth index* may therefore be expressed as $v(d/\sqrt{x})$ for any sector

of the valve. In Rudwick's terms, proliferation points and proliferation arcs are momentary and growth acceleration and relative growth index are cumulative.



TEXT-FIG. 1. Reconstruction of the primary growth vectors of *M. granulosa*, plotted from oriented fibres. Proliferation arcs dotte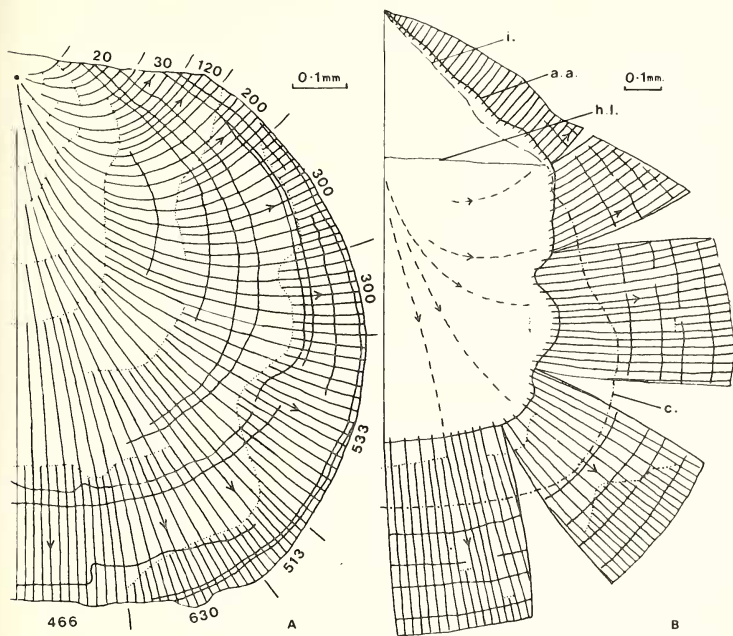d. Concentric lines represent visible growth-lines. A. Right half of a brachial valve. Numbers indicate relative growth indices in different sectors. B. Right half of a pedicle valve. Broken lines within the area of attachment represent the vector mosaic inferred by the brachial valve. Commissure projected stereographically to allow plotting of the primary growth vectors. The relative position of a.a. edge of the area of attachment, c. commissure and i. edge of interarea, plotted from cellulose acetate peels. h.l. hinge-line.

*Brachial valve*. The growth of the brachial valve of *M. granulosa*, when expressed in the manner outlined, shows a marked radial pattern with a high relative growth-rate anterolaterally (text-fig. 1A). For the reasons outlined in Williams and Wright (1963) it is considered that it is only necessary to plot the data for one-half of the valve.

The validity of the above interpretation obviously rests on the assumption that the proposed association of fibre orientation with deposition of the primary layer is correct. The author is alive to the possibility that in the material investigated, the growth vectors

are not recorded from the exposed ends of primary fibres but from crystallites growing on their outer ends. However, the fibre orientation pattern shows a remarkable constancy in the thirty external brachial surfaces examined. Even if the development of the fibres is diagenetic, the constancy of their orientation pattern must be in some way connected with the microstructure of the primary layer, most probably the crystallographic orientation of the primary fibres themselves (Cloud 1942, p. 24).

*Pedicle valve.* Analysis of the growth-lines of the pedicle valve of *Thecidiopsis* (Nekvasilová 1967) has enabled determination of the mode of development. Study of *M. granulosa* shows that the pedicle valve exhibits the same development régime, which, when advanced, produces an almost linear pattern masking the radial growth typical of brachial valves. After the development of the area of attachment and presumably in response to environmental influence, material is added to the anterior and anterolateral regions of the pedicle valve much more rapidly than in the other regions so that the angle between the plane of the commissure and the plane of the area of attachment changes rapidly and the anterior and antero-lateral regions of the shell develop rapidly without appreciably increasing the length of the commissure. This means that the deposition of the primary layer of the pedicle valve although remaining normal to the valve margin shows a distinctly linear growth orientation anteriorly (text-fig. 1b). In Rudwick's terms therefore, the growth of the shell of *M. granulosa* is characterized by a declining vertical component in the brachial valve and an increasing vertical component in the pedicle valve, a cumulative growth pattern which obviously serves to lift the anterior gape away from the substratum (Pl. 18, fig. 4).

*Secondary layer.* As shown by Williams the secondary shell consists essentially of fibres arranged with their long axes at a low inclination to the internal surface of the primary layer and overlapping to a greater or lesser extent according to the angle of inclination, usually about 10°. By plotting the orientation of the long axes of exposed parts of secondary fibres, Williams (1968a, pp. 10–15) has demonstrated a discernible lineation in several genera. Construction of a secondary growth mosaic for *M. granulosa* shows the existence of the same spiral arc arrangement in which there is a relatively constant deflexion of the secondary fibres (text-fig. 2). The pattern is modified anteriorly in the brachial valve by the development of the relatively very thickened anterior of the median septum. There is no sign of peripheral reorientation normal to the shell edge but this may simply be the result of the disruptive influence of the tubercle cores. Williams (1966, p. 1148) notes the blurring of the pattern in areas of excessive calcite deposition in terebratuloids. In the pedicle valve also, the spiral arc pattern is modified anteriorly by the development of the crescentic tubercles. However, although Williams is able to demonstrate the bulk migration of the mantle in the direction of growth (1968a, p. 8) in order to account for the inclination of secondary fibres, the reason for the migration has not been explained. Study of his text-figure makes it apparent that it is impossible to extend the fibre series anteriorly or posteriorly without changing their inclination. The situation is further complicated by trying to impose the model on a convex shell. There is ample figured evidence, however, to show that his account of fibre shape must be correct. The solution to the problem must, therefore, lie in the orientation of the fibres themselves. The length of the fibres in any zone of the shell seems to remain fairly constant, suggesting that the cells of the epithelium secreting them have a standard life and

secretory activity. Obviously the rate of cell division in the mantle groove must vary to account for the growth characteristics of the shell. If the organization of the cells is such that the calcite of the secondary fibres is secreted at a fairly constant rate, areas showing
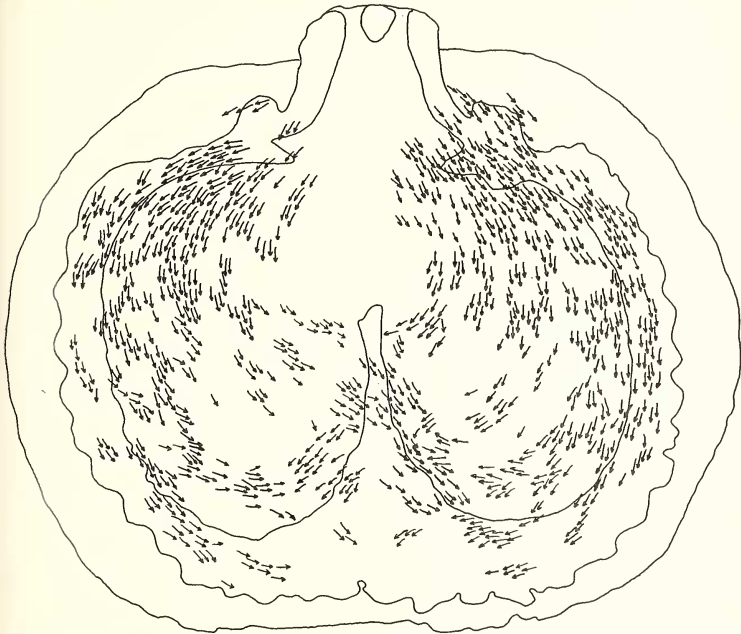


TEXT-FIG. 2. Reconstruction of the secondary growth mosaic of *M. granulosa*, plotted from twenty-five superimposed peels. Solid outline represents the position of the sub-peripheral rim, median septum, and cardinal process.

a relatively slow vectoral primary growth rate, i.e. postero-lateral sectors, must suffer from a build-up of secondary shell, unless the fibres are deflected away from the primary growth vectors in order to prevent the shell from becoming excessively thickened. Conversely the fibres may be deflected towards areas where thickening of the shell is taking place, such as the development of the median septum (text-fig. 2). This orientation deflexion of the secondary fibres away from sectors of relatively decelerated deposition of primary shell material would readily explain the forward migration of the secreting cells and the difference in orientation between the vectors of the primary and secondary layers (text-figs. 1A, 2).

## DEVELOPMENT OF SPECIFIC STRUCTURES

*Development of the sub-peripheral rim.* Very little progress regarding the determination of the microstructure of the brachial valve was made until the mode of development of the sub-peripheral rim was appreciated. Williams (1968*a*, p. 50) described local resorption in *Lacazella* and resorption is found to play an important role in *M. granulosa*. Ontogenetic studies (Baker 1969) show that the sub-peripheral rim appears at the preforbesiform stage of development and subsequently occupies the same position relative to the valve margin, irrespective of the size of the valve. As the sub-peripheral rim is too prominent to be submerged by subsequent secondary shell deposition, it must migrate outwards. Evidence that the migration is accomplished by development at the external margin of the rim and resorption along its inner margin will be presented later. The subperipheral rim is tuberculate and the generative zone of the tubercles appears to be where the secretory activity of the outer epithelial cells changes from the deposition of primary to the deposition of secondary fibres.

*Development of the hemispondylium.* Elliott (1948) noted the presence of a structure in the floor of the pedicle valve of *Bifolium faringdonense* (Davidson) to which he gave the name hemispondylium. In his opinion, the structure was not formed by the fusion of dental plates. Elliott also noticed the presence of what might almost be called dental ridges, buttressing the hinge teeth internally but adopted the view that they played no part in the formation of the muscle supports (spondylium) as in other brachiopods, a view confirmed by the present work. Some specimens of *M. granulosa* however, show that the buttressing ridges which may represent rudimentary dental plates, are continuous with the upturned outer edges of the hemispondylial plates (Pl. 18, fig. 6). This arrangement is an interesting feature and may be homologous with the ankylosed median septum–dental ridge structure of the davidsoniacean *Orthotetes*.

Sectioned material enables resolution of the problem. Forms with a supporting septum have the appearance of possessing a spondylium simplex (text-fig. 3A–C, G). However, forms with a sessile hemispondylium show quite clearly that the dental ridges simply merge with the floor of the valve (text-fig. 3D–F, H). There can be no doubt therefore, that Elliott's interpretation is correct and that the hemispondylial plates are not formed by the fusion of dental plates but from secretion of secondary shell by the outer epithelium adjacent to the supporting septum. The dental ridges may or may not unite with them depending on the growth habit of the valve. In forms with well-developed dental ridges it is possible to obtain sections which are strikingly similar to sections through the umbonal region of pedicle valves of *Derbyia* (Williams *et al.* 1965, H404, fig. 261 D). As Nekvasilová (1964) has recorded in *Lacazella* (*B*) *lacazelliformis* (Elliott) and as Elliott has recorded in *B. faringdonense*, the hemispondylium is present in the smallest valves studied and may be sessile or supported by a median septum. Rare specimens may show the hemispondylial plates supported by a double septum anteriorly. A single specimen of *M. granulosa* shows the hemispondylial plates supported by three septa whilst another (Pl. 19, fig. 1) shows a reticulate support. The form of the hemispondylium may be correlated with the form of the area of attachment and is apparently related to muscle efficiency (Elliott 1948, p. 20).

*Development of the crescentic tubercles.* Post-forbesiform and adult pedicle valves are characterized by the development of structures along the internal edge of the valve
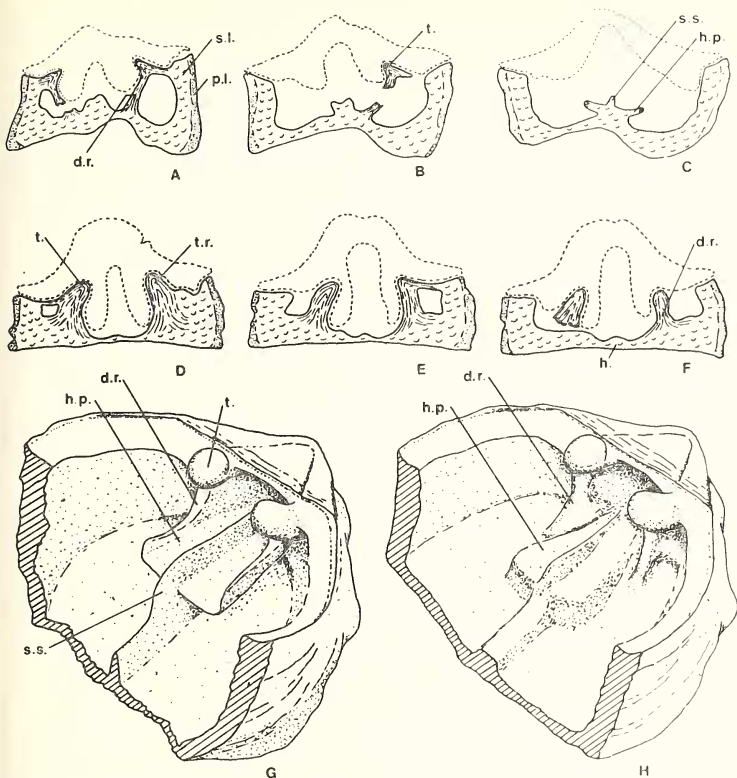
TEXT-FIG. 3. A–C. Three serial sections through *M. granulosa* to show the form of the supported hemispondylium. D–F. Three serial sections, showing the form of the sessile hemispondylium. G. Three-quarters profile reconstruction of a supported hemispondylium, showing the dental ridges continuous with the hemispondylial plates. H. Three-quarters profile reconstruction of a sessile hemispondylium, showing the dental ridges merging with the floor of the valve. Outline of brachial valve dotted. d.r. dental ridge, h. root of sessile hemispondylium, h.p. hemispondylial plate, p.l. primary layer, s.l. secondary layer, s.s. supporting septum, t. tooth, t.r. tooth ridge.

margin (Pl. 18, fig. 2; Pl. 19, fig 2). which Elliott in *B. faringdonense* has called sub-pustulose marginal ornament. In *M. granulosa* these structures can be shown to be modified tubercles and are thought to be of considerable importance. As their shape is quite characteristic it is proposed to designate them crescentic tubercles. They appear

to be most strongly developed in the anterior and antero-lateral sectors of the valve and show a development pattern entirely different from that of the tubercles of the sub-peripheral rim. Crescentic tubercles do not appear until the anterior of the pedicle valve begins to grow away from the attachment surface. They apparently grow simply by the incremental addition of material at their distal ends and the secreting cells must occupy an invagination of the outer epithelium so that the tubercle cores stay slightly in advance of adjacent outer epithelial secretory cells. Their relationship with adjacent secondary fibres would indicate that their long axes are not quite parallel with the internal shell surface but inclined dorsally inwards at an angle of about 2°. This development pattern of the crescentic tubercles is obviously related to the maintenance of a constant orientation relative to the tubercles of the sub-peripheral rim (text-fig. 6A, c).

### DETAILED MICROSTRUCTURE

As already noted, *Moorellina granulosa* (Moore) offers conclusive proof that in some Jurassic thecidellinids at least, the shell was differentiated into primary and secondary layers. The primary layer is best seen in the pedicle valve where it is relatively much thicker than in the brachial valve. It is possible that in some specimens the thin primary layer may occur only sporadically as in orthoids and strophomenoids where its absence is attributable to wear of a very thin layer. The possibility of the removal of the primary layer is important in the interpretation of occasional pitted structures, described later, occurring in the outer surface of some brachial valves.

The primary crystallite mat gives the typical fibrous, transverse (Pl. 19, fig. 3) and pitted, horizontal (Pl. 19, fig. 4) sections described by Williams. Transverse sections through secondary fibres show typical cross-sections (Williams 1968a, p. 9) with the exception that the lateral areas are much reduced so that a sub-hexagonal pattern is produced (Pl. 19, fig. 5). This standard shape appears to persist throughout the secondary layer of the pedicle valve but shows some modification in the brachial valve. Patches of fibres in the brachial valve show dorso-ventral flattening distally so that they develop
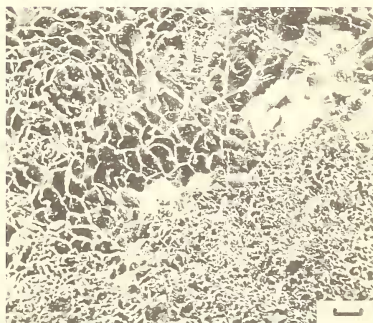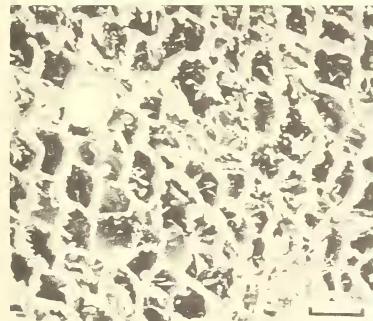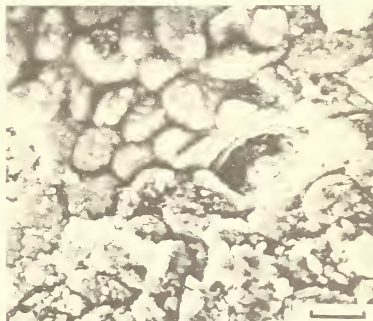
TEXT-FIG. 4. A. The distribution of the tubercle cores (dotted) in the brachial valve of *M. granulosa*, plotted from twenty-five superimposed peels. The core distribution inside the sub-peripheral rim, outlined, indicates the areas of the brachial cavities where resorption has occurred. B. Diagrammatic representation of the probable mode of migration of the sub-peripheral rim during growth. C. Normal and flared transverse mosaics. D. Diagram to show the shape of an individual fibre. b.c. brachial cavity, k. keel, l.a. lateral area, p.l. primary layer, r.g. rim generation zone, r.r. rim resorption zone, s.l. secondary layer, s.p.r. sub-peripheral rim, t.c. tubercle core.

flared ends (text-fig. 4c, d). The possibility that these were merely apparent transverse sections, produced by fibre reorientation was checked against horizontal longitudinal sections through fibres. The flared secondary fibres have a characteristic strap-like appearance and are up to three times (10–12 $\mu$) the width of normal fibres. It is possible that the modified fibres are associated with muscle scars but this could not be confirmed in the material studied. The location of the sections however, would suggest that the fibres occur in zones of the valve which were not areas likely to be associated with muscle attachment.

The variability of the fibres in section and the consequent possibility of misinterpretation of sections has been noted by Williams (1966, p. 1148). The present work has been hindered by the same rapid changes of fibre orientation. Studies indicate that orientation variation in the secondary layer may occur at different depths, in different sectors of a valve, and that the microstructure of the brachial and pedicle valves of the same animal may show significant differences. For this reason it is felt that all future plate figures must be accompanied by accurate data concerning the orientation of sections through the specimen and the exact location of the section on the shell. The author has attempted to present such data in a concise form in the plate explanations, to enable other workers to avoid or duplicate these sections in subsequent investigations.

Relatively large areas of the brachial cavities of *M. granulosa* are formed by the progressive resorption of the sub-peripheral rim (text-fig. 4a, b). As a result of resorption in these areas, the fibre orientation persisting at the bases of former sub-peripheral rim tubercles is exposed on the internal surface of the valve, producing a very disturbed pattern (Pl. 20, figs. 1, 2). Once the significance of rim resorption had been appreciated, it was realized that undisturbed secondary mosaic would only be seen in areas which were not affected by shell resorption. This suggested three possible sites, (*a*) the border

EXPLANATION OF PLATE 20

Stereoscan photomicrographs of *Moorellina granulosa* (Moore) except figs. 7 and 8. Material of all figures coated with evaporated aluminium before photography.

Fig. 1. Interior view of a brachial valve (37519), showing an endopuncta and disturbed secondary mosaic, right, in the area affected by resorption of the sub-peripheral rim. Scale represents 5 $\mu$.

Fig. 2. Stereoscanned cellulose acetate peel (37520), showing the disturbed secondary layer of the brachial valve and the development of flared fibres, lower centre. Section orientation: parallel with the plane of the antero-lateral surface. Section location: right antero-lateral sector 0·12 mm. from the external surface of the valve. Scale represents 25 $\mu$.

Figs. 3–5. Stereoscanned cellulose acetate peel (37522).

Fig. 3. Section through the sub-peripheral rim showing the tubercle cores in cross section, offset by one half-phase. Two partially resorbed cores are visible along the inner margin of the rim, top left. Section orientation: parallel with the plane of the commissure. Section location: brachial valve, left antero-lateral sector 0·048 mm. from the distal ends of tubercles. Scale represents 20 $\mu$.

Figs. 4, 5. Isolated tubercle cores in areas of the brachial cavity affected by resorption of the sub-peripheral rim (fig. 4) and tubercle cores continuous with the primary layer (fig. 5, centre and lower right). Section orientation and location as in fig. 3, but 0·144 mm. from the distal ends of tubercles. Scale represents 20 $\mu$.

Fig. 6. Stereoscanned cellulose acetate peel (37523). Vertical section through the sub-peripheral rim showing tubercle cores in oblique section. Section orientation: perpendicular to the external shell surface at 85° from the long axis. Section location: brachial valve, right antero-lateral sector. Scale represents 30 $\mu$.
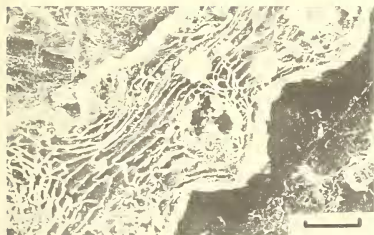
Figs. 7, 8. Stereoscan photomicrograph of the external surface of a brachial valve of *Moorellina ornata* (Davidson) (37524), showing detail of the structures interpreted as weathered tubercle cores. × 1000.
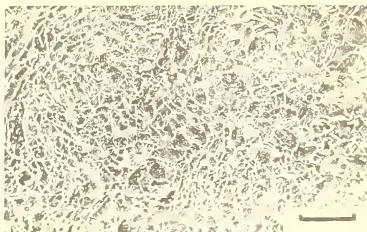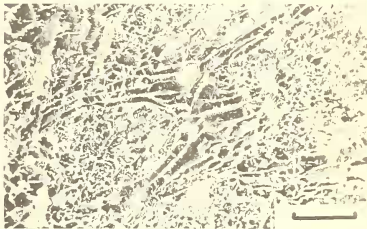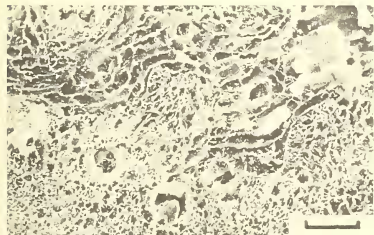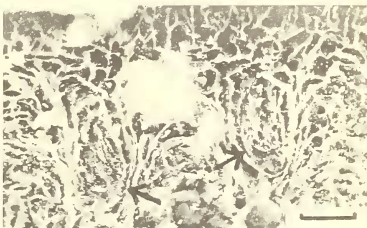
region outside the sub-peripheral rim, (*b*) the pedicle valve, and (*c*) the brachial cavities of pre-forbesiform (Baker 1969) individuals, where rim resorption had not yet begun. A detailed examination of brachial and pedicle valves was then undertaken with these considerations in mind. The border region has proved to consist entirely of primary shell and the mosaic on the inner surface of the pedicle valve is obscured by the development of crescentic tubercles. A pre-forbesiform brachial valve (37503) however, clearly shows traces of the internal mosaic of the secondary layer (Pl. 19, fig. 6).

The observed differences in the brachial and pedicle valves of *M. granulosa* have produced significant differences in microstructure and render it necessary that the microstructure of the two valves be described separately.

*Brachial valve.* A thin primary and a disturbed secondary layer associated with the development and migration of the sub-peripheral rim are present.

A detailed investigation of the tubercles of the sub-peripheral rim was undertaken. If the concept of resorption is correct, it should be possible to distinguish the remains of tubercle cores in areas of the brachial cavity formerly occupied by the sub-peripheral rim. Horizontal, transverse, oblique, and longitudinal sections were prepared in order to establish their presence. Horizontal serial sections (Pl. 20, figs. 3–5) show that the tubercles are cored structures and that the tubercle cores are, in fact, continuous with the material of the primary layer (Pl. 20, fig. 5). The tubercle cores may be regarded therefore, as being composed of primary shell type material. The question of whether the primary layer has suffered diagenesis has little significance as the material of this layer and of the tubercle cores has the same characteristics and may logically be considered to have the same origin. The author envisages localized patches of outer epithelium continuing to secrete primary shell. It seems probable that the mechanism of development is similar to that which controls the initiation of punctae, as tubercles also are normally, but not universally, offset by one half-phase (Pl. 20, figs. 3, 5). A plot of the tubercle cores in superimposed serial sections through a brachial valve of *M. granulosa* shows that they persist through several sections and are intimately connected with the development of the sub-peripheral rim. They do not appear in zones of the shell which may be logically considered to have been deposited prior to the appearance of that structure (text-fig. 4A). Horizontal sections through the sub-peripheral rim (Pl. 20, fig. 3) confirm that the tubercle cores originate near the mantle edge, in fact at the outer boundary of the sub-peripheral rim itself, and close to the point where the secretion of secondary shell begins. Subsequent isolation of eroded tubercle cores in the brachial cavities is brought about by the mode of development of the sub-peripheral rim during ontogeny (Pl. 20, fig. 4). Vertical sections (Pl. 20, fig. 6) show that the tubercle cores are inclined at a high angle, almost normal to the external shell surface, with a slight outward deflection.

That the tubercle cores of the brachial valve are composed of primary shell material would appear to be confirmed by occasional curious pitted structures occurring on the external surface of valves. Although these occur in *M. granulosa* they are better preserved in the Upper Oxfordian, *Moorellina ornata* (Moore) (Pl. 20, figs. 7, 8). Each pit has a central granular mound and may possibly be interpreted as some form of exopuncta. However, in the light of observations regarding the thickness of the primary layer and the fact that the tubercle cores are shown to be continuous with it, it would appear that what is actually seen is the outer boundary of the secondary layer, exposed by the

removal of primary shell. In which case, the apparent bands are the long axes of fibres and the central mounds of the pits are really weathered tubercle cores. This is supported by: (*a*) the orientation of the fibres is correct if they constitute part of a normal spiral arc, (*b*) they are the right thickness, about 4 $\mu$, (*c*) the granular nature of the central mound is the same as that of sectioned tubercle cores, (*d*) the diameter of the pits is the same as the diameter of tubercle cores in section, i.e. 25–30 $\mu$, and (*e*) they are too large to be normal punctae which have a diameter of only 8–10 $\mu$.

*Pedicle valve.* A well-developed primary and secondary layer are present. The primary layer thins posteriorly and the secondary layer shows modification anteriorly as a result of the growth habit of the valve.

Attempts to reconstruct a secondary mosaic in the manner described above, failed to produce a decipherable pattern because the secondary layer of the pedicle valve of *M. granulosa* is itself composed of two regions with regard to fibre orientation. There is an outer, essentially normal, spiral arc orientation and an inner layer in which the fibre orientation is intimately bound up with the development of the crescentic tubercles (Pl. 21, figs. 1, 2). In the lateral and postero-lateral sectors of the valve, the secondary fibres show a normal spiral arc arrangement. In the zones of the anterior surface adjacent to the area of attachment, the orientation of the fibres of both regions of the secondary layer appear to follow the primary growth vectors and produce typical longitudinal sections through fibres (Pl. 21, fig. 3). However, as growth of the pedicle valve proceeds away from the substratum, the secondary layer is differentiated into outer and inner regions. The orientation of the fibres in the outer region changes in such a way that they come to lie almost parallel with the commissure. Longitudinal

EXPLANATION OF PLATE 21

Stereoscan photomicrographs of specimens of *Moorellina granulosa* (Moore). Material of all figures coated with evaporated aluminium before photography.

Fig. 1. Stereoscanned cellulose acetate peel (37520). Transverse section through a pedicle valve showing the orientation of the outer fibres of the secondary layer and the reniform tubercle cores. Section orientation: parallel with the plane of the commissure. Section location: left antero-lateral sector, 0·4 mm. from the distal ends of the tubercles. Scale represents 50 $\mu$.

Fig. 2. Stereoscanned cellulose acetate peel (37521). Section through the secondary layer showing fibres deflected by the crescentic tubercles. Section orientation: parallel with the anterior surface. Section location: pedicle valve, anterior surface, 0·168 mm. from the external surface. Scale represents 20 $\mu$.

Figs. 3, 4. Etched surface prepared from polished block (37516). Section orientation and location as in fig. 3 (Pl. 19). Fig. 3 shows the primary layer, bottom and detail of the secondary fibres in longitudinal section. Fig. 4 shows reorientation of the fibres of the outer region of the secondary layer to give almost transverse section. The elongate fibres (oblique section), upper left, represent a tubercle core sectioned near the axis. Scale represents 10 $\mu$.

Fig. 5. Stereoscanned cellulose acetate peel (37521). Section through the secondary layer showing the fibrous cores of the crescentic tubercles. Section orientation and location as in fig. 2, but 0·096 mm. from the external surface. Scale represents 50 $\mu$.

Fig. 6. Interior view of the anterior surface of a pedicle valve (37515) showing the arrangement of the punctae in rows relative to the crescentic tubercles. × 50.

Fig. 7. Stereoscanned cellulose acetate peel (37523). Transverse section through the ventral umbonal region showing the plugged pedicle opening and dorsally exposed pedicle sheath. Section location: 0·08 mm. from the umbo. Scale represents 50 $\mu$.
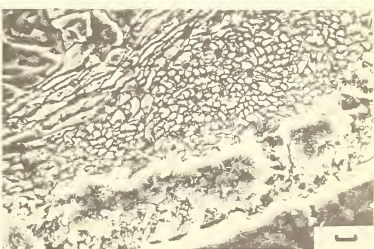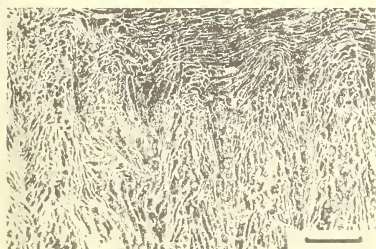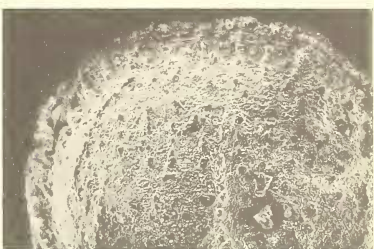
Fig. 8. Retouched photomicrograph of fig. 7.
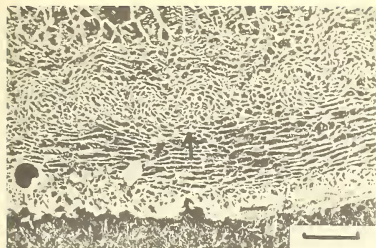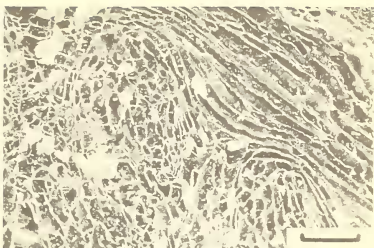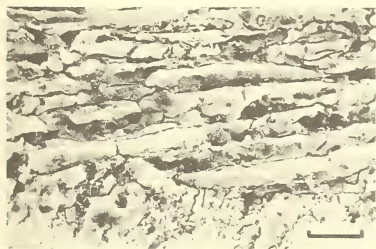
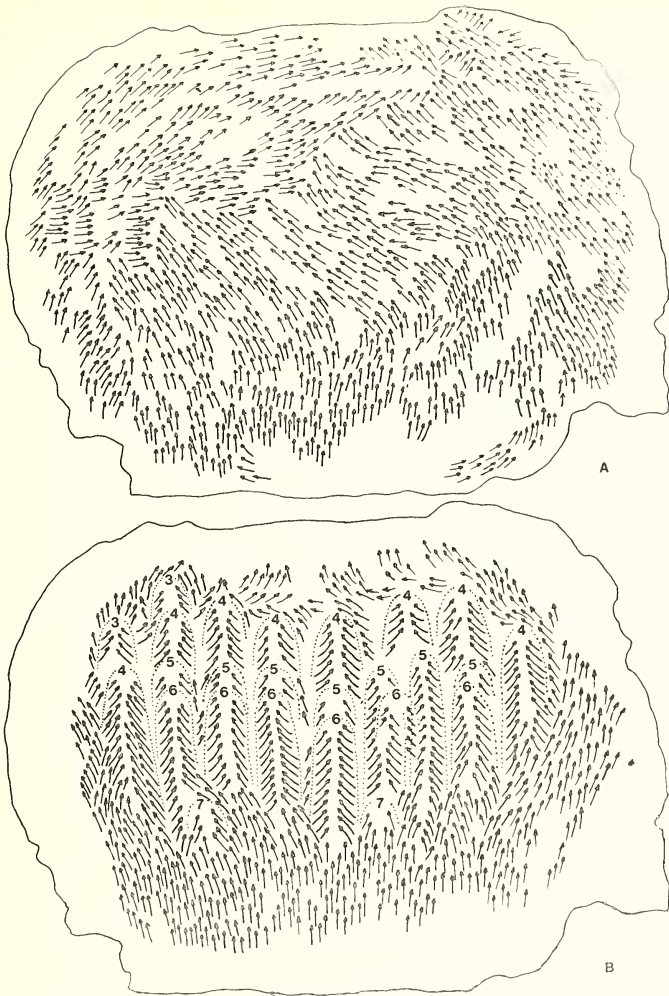TEXT-FIG. 5. Reconstruction of the fibre orientation of the outer and inner regions of the secondary layer of the free anterior of the pedicle valve of *M. granulosa*, from eight superimposed peels. A. Fibre orientation of the outer region. B. Fibre orientation and tubercle cores of the inner region. Numbers indicate the position of the tubercles in successive peels, from the internal surface of the valve.

sections through these zones produce almost transverse sections through the fibres of this outer layer (Pl. 21, fig. 4).

With this information available the growth mosaics of the two regions were fairly easily reconstructed by plotting the fibres of the outer and inner regions separately. This was achieved by plotting the primary/secondary layer junctions of serial sections, together with the orientation direction of the fibres adjacent to the junctions. The mosaic produced (text-fig. 5A) was interpreted as representing the growth mosaic of the outer region of the secondary layer of the anterior surface of the pedicle valve. Similarly, a re-plot of the remaining fibre orientation on each serial section, i.e. omitting those plotted in text-fig. 5A, was interpreted as representing the growth mosaic of the inner region of the secondary layer (text-fig. 5B). A suggested explanation for this anterior differentiation is offered later, as it can be shown not to be present throughout the whole of the secondary layer.

As in the brachial valve, the structure of the crescentic tubercles was investigated with the aid of transverse, horizontal, oblique, and longitudinal serial sections. In longitudinal sections the tubercles are seen to be composed entirely of fibrous cones (Pl. 21, figs. 2, 5) deflecting the other fibres adjacent to them. In transverse section (Pl. 21, fig. 1) the tubercles exhibit a characteristic reniform shape. The presence of these structures may be of profound significance and their implication is discussed later.

Compilation of the features exhibited by serial sections at various orientations allows reconstruction of the microstructure of the shell of *M. granulosa* (text-fig. 6A–C).

*The pseudodeltidium and pedicle sheath.* Study of *Lacazella* (Williams *et al.* 1965) indicates that neither the pedicle nor its muscle system is developed. The structure of the strophomenoid pseudodeltidium is still imperfectly known but it is now generally agreed that it consists of primary and secondary material and was secreted between the teeth ridges by the outer epithelium. Ventral umbonal regions of well-preserved specimens of *M. granulosa* were carefully sectioned in an attempt to resolve the problem of the fate of the pedicle opening in Jurassic thecidellinids. Owing to the mode of growth of the area and the minute proportions of the structures involved, it was difficult to distinguish the pseudodeltidium at all. Of the limited number of specimens in which it could be recognized, only three showed any discernible microstructure. In these specimens, transverse sections close to the ventral umbo show the presence of a minute pore 50 $\mu$ in diameter and apparently plugged by calcite having a different orientation from that of the pseudodeltidium (Pl. 21, figs. 7, 8). The pore appears at about 0·06 mm. from the posterior of the pedicle valve and close to the area of attachment (text-fig. 7c) in what must be regarded as a supra-apical position (text-fig. 7H). It appears to be surrounded laterally and dorsally by a collar or ring of material in which the fibres show a concentric orientation in the plane of section. The dorsal surface of the ring is exposed externally and is obviously the structure interpreted as a pseudodeltidium. In subsequent sections the pore migrates dorsally away from the area of attachment and the ring increases in size, still maintaining its dorsally exposed surface (text-fig. 7c–f). Continuity of the structure through several sections reveals that it is really a calcareous tube, which, if the plugged pore represents the site of the atrophied pedicle opening, may be regarded as a form of pedicle sheath which initially closed the delthyrium. At about 0·14 mm. from the umbo the structure terminates (text-fig. 7g) and is replaced by the ventral umbonal cavity, housing the posterior tip of the cardinal process. The space between the tooth
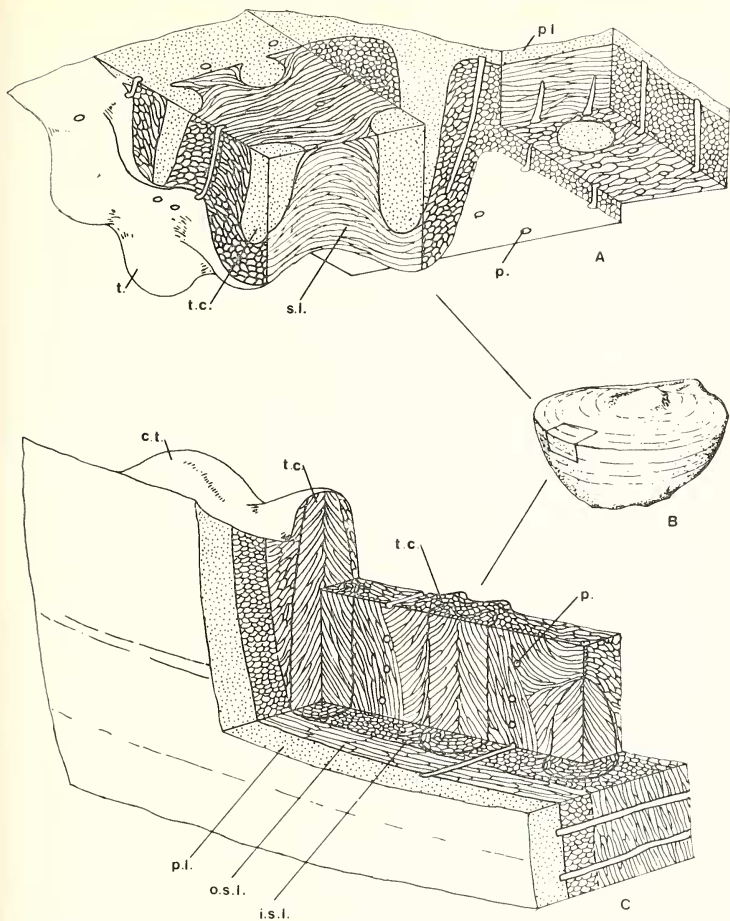
TEXT-FIG. 6. Diagrammatic reconstruction of the shell microstructure of *Moorellina granulosa* (Moore). A. Block diagram showing the microstructure of the brachial valve. B. Complete specimen showing relative position of the reconstructed segments. C. Block diagram showing the microstructure of the pedicle valve. c.t. crescentic tubercle, i.s.l. inner secondary layer, o.s.l. outer secondary layer, p. puncta, p.l. primary layer, s.l. secondary layer, t. tubercle, t.c. tubercle core.